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SEXUAL SELECTION BY FEMALE CHOICE IN POLYGYNOUS ANIMALS

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INTRODUCTION

Darwin's theory of organic evolution identifies two forms of selection that occur in the wild: natural selection, involving the adaptation of a population to its biotic and abiotic environment, and sexual selection, resulting from competition for reproductive access to the other sex (27, 28). Sexual selection arises through a direct struggle between members of the same sex (typically males) and through the mating preferences of one sex for the other (typically females for males). Darwin developed the concept of sexual selection to account for many spectacular phenomena, such as the plumage of male peacocks, that seem incompatible with natural selection. He wrote that "sexual selection has played an important part in the history of the organic world," and devoted most of his largest book to the subject.

Despite this early impetus, sexual selection in general, and female choice in particular, were largely neglected by biologists for almost a century following Darwin's work (48, 67, 97, 111). The reasons for this have yet to be fully understood but must in part have been caused by the skepticism of Wallace (133) and Huxley (63), who discounted Darwin's ideas on the subject. Important contributions during this hiatus were made by Poulton (105) and Belt (8), who added their comparative observations to Darwin's, and by Fisher (45), whose verbal theory has been a source of inspiration and controversy ever since. Over the last two decades a major resurgence of work on sexual selection has occurred. Evolutionists have reexamined Darwin's ideas and are now much more impressed by their cogency. Many current discussions of sexual selection by female choice are centered around a lively debate. Given the vacuum of thought on the subject for the first part of the

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twentieth century, it is not surprising that divergent schools of thought about sexual selection have developed.

The primary goal of this review is to summarize the controversy that dominates many current discussions of sexual selection by female choice. This is not a general survey of sexual selection, but rather an outline of the empirical and theoretical knowledge relating to this controversy. It focuses on polygynous species, since in those species the results of sexual selection are most obvious and most extreme. In the interests of simplicity, it avoids interesting but complex related issues such as direct male-male competition and sexual selection in monogamous species.

THE CONTROVERSY

Current thinking about sexual selection can be roughly divided into two schools. These are the "good genes" school, which postulates that mate choice evolves under selection for females to mate with ecologically adaptive genotypes, and the "nonadaptive" school, which holds that preferences frequently cause male traits to evolve in ways that are not adaptive with respect to their ecological environment.

The good genes school has its historic foundations in the adaptationist approach to evolutionary biology that developed in the 1960s. An important influence was the large body of avian studies which show that mating systems are strongly molded by food, nest sites, and other resources that females need for reproduction (38). In this context, it was perhaps natural to suggest by analogy that females might receive genetic "benefits" from their mates in those species where males do not contribute material benefits to the females or their offspring. This reasoning lead Trivers, for example, to state in 1972 that "where the male invests little or nothing beyond his sex cells, the female has only to decide which male offers the ideal genetic material for her offspring" (129). The theme of all such arguments is that preferences evolve adaptively, favoring males that carry genes that promote survival. This has been the guiding concept for most discussions of sexual selection in the last two decades (e.g. 12, 89, 100, 128, 130, 139).

The nonadaptive school has a very different view of how sexual selection works. Its proponents argue that both data and theory lead to the conclusion that female preferences for ecologically adapted males are generally not what evolution produces. Numerous evolutionary processes, some even unrelated to mating, can lead to behaviors that bias females towards certain kinds of males. Often these "preferences" are for kinds of males that are different from those that natural selection favors. This leads to a conflict between the forces of natural and sexual selection acting on the males, causing them to evolve to a compromise state that is maladaptive with respect to what natural selection acting alone would produce.

The good genes and nonadaptive schools thus differ in their expectations about how evolution operates under sexual selection. The critical difference is in their expectations about how female mating preferences evolve—the good genes school argues that they evolve to favor ecologically adapted males, while the proponents of the nonadaptive school hold that preferences usually evolve in maladaptive ways. This difference is so fundamental that it would seem the controversy could be resolved directly by appealing to the data.

THE EVIDENCE

Sexual selection by female choice involves the evolution of two characters, a male secondary sexual *trait* and a female mating *preference*. Since much of the confusion on this topic has come from failing to distinguish clearly between the evolutionary forces acting on the trait and those acting on the preference, I emphasize the distinction by discussing each of the two characters separately.

The Male Trait

EVIDENCE OF SEXUAL SELECTION BY FEMALE CHOICE What evidence is there of sexual selection by female choice acting on male traits? By far the largest body of data is from comparative studies, in the tradition of Darwin (28; see 8, 37, 105). An increasing number of careful field studies have now directly demonstrated sexual selection by female choice in natural populations. Experimental studies are important because they can show directly what male traits are used by females in mate discrimination. Andersson (3) performed an elegant experiment in which he surgically manipulated the length of the extravagant tails of male widowbirds. Results show that males with longer tails attract more nesting females. Ryan and his coworkers (summarized in 111) have experimentally demonstrated that male tungara frogs which add a "chuck" component to their calls are more attractive to females than males that do not. Studies of field crickets (57) have established that males with longer calling-bout durations are preferred by females. Dozens of studies have proved that female preferences operate in many other species as well (e.g. insects: 128, 135; fish: 40, 43, 61, 72, 120; frogs: 124; birds: 13, 49; see 116 for further references), showing that female choice is a powerful evolutionary force in many polygynous species.

DO NATURAL AND SEXUAL SELECTION ON MALE TRAITS OPPOSE EACH OTHER? Fisher (45), in the first modern discussion of sexual selection, considered how evolution might establish preferences for maladaptive males. We can, however, imagine a world in which it is otherwise: Females might tend to mate with the most viable males, as predicted by the good genes school. (A short semantic digression: When discussing this topic it is helpful to avoid the term "fitness." It is circular, for example, to ask whether a female mates with the most fit male, since by choosing a male as a mate the female by definition increases his fitness. Terms such as survivorship, viability, and mating success are much less ambiguous in this context.)

There are three possible situations. The first is that envisioned by the nonadaptive school, in which natural and sexual selection favor different forms of the male trait. Survival, for example, might select for males with short tails, while females prefer to mate with males that bear long tails. The second case is one in which natural and sexual selection favor the same intermediate expression of the male trait. This will occur when stabilizing viability selection and female preference both favor males of intermediate size. In the third case, natural and sexual selection both favor the same extreme form of the male trait. Males that grow fastest might survive better (because they avoid predators, say) and also get more matings because females prefer mating with larger males. Here natural and sexual selection continually favor faster growth. The second and third cases are similar in that natural and sexual selection reinforce each other. The third case differs from the first two in that the male trait experiences constant directional selection.

Natural selection and sexual selection opposed The oldest argument that natural and sexual selection commonly oppose each other follows the logic of Darwin (27, 28), who in fact invented the concept of sexual selection in order to account for traits that appear to be inconsistent with natural selection.

There are now a number of field studies that have directly demonstrated cases in which natural and sexual selection are opposed. The most dramatic are those in which male displays attract not only females but also predators. Playbacks of male calls show that a predatory bat locates male tungara frogs using the same components of their calls that female frogs use (111). The advertisement songs of male crickets attract parasitic flies as well as females (20). Among fish, male guppies (39, 40, 56) and sticklebacks (93, 120) that contrast visually with their environment are more likely to be eaten by predators but are favored by females in mating. Predaceous fireflies of the genus *Photuris* home in on the luminescent flashes that males of other firefly species make while trying to attract conspecific females (82). In these examples, increased development of the male secondary sexual trait leads inevitably to increased male mortality.

Other studies also suggest that male traits increase mortality but have not conclusively determined how they do so (e.g. 98, 119). The energetic costs of mating displays for males of some species represent a substantial fraction of their total energy budget (54, 111, 113); thus, there may be selective costs. No study, however, has yet determined if natural and sexual selection by female choice quantitatively balance each other. It would be very interesting to apply existing methods for measuring selection in natural populations (7, 41, 78; see also 125) to this question.

The comparative method supplies several lines of evidence suggesting that natural and sexual selection are opposed in several groups of animals. Darwin built his case for sexual selection on this kind of data. He observed that display traits are typically restricted to one sex, not expressed in juveniles, and used only during the mating season, all of which suggest that these traits are not advantageous under natural selection. Later workers have added to these observations (e.g. 37, 103, 105). A particularly interesting example is the female-limited mimicry in butterflies that suggests female mate choice prevents males from evolving adaptive mimetic color patterns (8, 131).

Thus, a substantial body of data documents cases in which females prefer deleterious male traits, as the nonadaptive school would predict.

Natural and sexual selection favor the same intermediate expression of the male trait In the second of the three situations, natural selection and female preferences favor the same intermediate phenotype of the male trait. The result is that natural and sexual selection reinforce each other, an outcome that is compatible with the good genes view.

Very few examples fall in this category. Mason (87) found that male oak moths that successfully mate are less variable in wing length than the population of unmated males. Since it appears that female choice is at work and it is plausible that stabilizing natural selection also acts on wing length, this example is a candidate case. Butlin et al (19) showed that female crickets favor calls that have syllables of intermediate length. Doherty & Gerhardt (32) report that female spring peepers prefer males who call at intermediate frequencies. While both of these last two studies have clearly demonstrated sexual selection for intermediate male traits, it is not clear that natural selection favors any particular value of those components of the male trait. That is, natural selection probably favors decreased male calling but may not discriminate between males that call with different syllable lengths or at different frequencies. These examples therefore may not be of natural and sexual selection reinforcing each other.

This situation is probably underrepresented in the literature because biologists have focussed on the spectacular cases in which male traits are highly exaggerated. Despite this bias, it seems unlikely that this is the most common of the three situations being considered.

Natural and sexual selection favor the same extreme expression of the male trait In the last of the three situations, natural and sexual selection reinforce each other by favoring ever more extreme expression of the male trait. This is thought to be a common or even typical situation by many proponents of the good genes school.

Several studies have found that certain males are both more healthy or vigorous and are preferred by females as mates. In sulphur butterflies, males with certain biochemical genotypes are stronger fliers and also have higher mating success (135). Female guppies favor matings with males that have bright carotenoid pigments, and brightness may be influenced by foraging success (39). Hamilton & Zuk (55) suggest that in birds and probably many other animals, males that are diseased or parasitized may tend to have paler coloration and consequently be less preferred by females. Males in *Drosophila subobscura* that are outbred court vigorously and are mated by females more often than inbred males (88). These and other observations suggest that females of many species tend to mate with males that are vigorous and/or that survive well, as predicted by the good genes school.

THE DATA REINTERPRETED A parsimonious conclusion from this survey might be that there are some data that contradict the good genes expectations and others that contradict the expectations of the nonadaptive school. This conclusion grossly underestimates the ingenuity of both schools in interpreting the data.

Interpretation of the good genes school A simplistic version of the good genes argument is that females generally prefer male traits that increase survival (e.g. 73). Were this true, it would be very difficult to explain Darwin's basic observation that expression of display traits is usually limited to mature males.

Most current good genes hypotheses acknowledge this point and appeal to a much more sophisticated argument. First, it is agreed that male traits themselves usually do decrease survival. The numerous cases in which male advertisement increases the risk of predation and so forth are acknowledged. But this does not necessarily imply that females have evolved preferences for maladaptive males. Bright male colors may encourage predation, the argument goes, but brightness tends to be correlated with other characters that enhance viability. Females mating with bright males then receive an evolutionary advantage by passing these other good genes of the bright males on to their offspring. The evolution of bright male colors is seen as a byproduct of the adaptive evolution of the preferences.

A widely-discussed version of these second-generation good genes hypotheses is Zahavi's "handicap" mechanism (144). Zahavi argued that bright males are usually also vigorous (high viability) with respect to other characters; otherwise they would not have survived to maturity. Females are selected to mate with the bright ("handicapped") males, because by choosing such a mate she will also tend to be choosing other genes for high viability, which will be passed to her offspring. Other proposals share similarities with the handicap mechanism. Numerous people have suggested that females that mate with older males will tend to mate with high viability genotypes, since older individuals have passed the tests of selection (e.g. 52, 129). Alternatively, the expression of the male trait could be conditional on the overall genetic "quality" of the male, so that physiological mechanisms cause the trait to become more exaggerated in individuals that carry good genes (4, 34, 39, 55, 96, 130). These arguments are similar in that they conclude that preferences for exaggerated male phenotypes receive an evolutionary advantage by becoming associated with adaptive (high viability) genotypes, and that exaggeration of the male trait is just a side-effect of this process. Data showing that the male trait itself decreases survival can therefore be accommodated by the good genes school.

Interpretation of the nonadaptive school Symmetrically, examples in which natural and sexual selection reinforce each other can be accommodated by the nonadaptive school. Consider the studies by Watt et al of butterflies (135) showing that males carrying certain biochemical genotypes are both more vigorous (e.g. are stronger fliers) and more likely to receive a mating advantage. Females tend to mate the most vigorous male genotypes more often because those males are persistent in courtship. The critical point here is that it is not courtship persistence itself that increases male survival, but rather other characters such as flight ability that are correlated with it. If the other characters were held constant, it is likely that the male trait would decrease survival because of the risk of predation, energetic demands, and other costs. Of the studies discussed above, those that have measured the effects of male traits while controlling for variation in other characters have shown the traits to be deleterious; none has shown them to enhance survival.

The deleterious effect of the male trait therefore can be masked by variation in other characters that have a positive effect on both survival and the expression of the male trait. Understanding sexual selection in these cases requires consideration not only of the trait and the preference, but also of the additional characters. Theoretical studies discussed below suggest that the presence of these additional characters does not cause evolution to work in the adaptive way envisioned by the handicap hypothesis.

Whenever a preference for louder, brighter, or more extreme male traits is established by any mechanism, adaptive or not, males that are the physiologically most competent will have a mating advantage. Compensatory modifications of the males to cope with the demands of the preference, such as increased aerobic scope and enlarged musculature, will often evolve (52, 113). Males that are disease- and parasite-free will often be more able to meet preference criteria that require large energetic outlays. Whether the preference itself became established because females mating these more vigorous males received an evolutionary advantage is an entirely different question. That females happen to mate more viable males could be an incidental side-effect of the preference, rather than the cause of the preference. The observation that females don't mate with road-killed males does not mean that their behavior evolved specifically to produce that effect!

It is clear that, despite numerous attempts to do so, it is impossible using only information about the male trait to infer how the female preference evolves. Patterns of selection and evolution of the male trait that are consistent with both schools are so varied that much of the data can be interpreted as support for either. In particular, the prediction that more vigorous males will mate more successfully is made by both schools. The crux of the debate, and its resolution, lies in understanding how the preference itself evolves. What, then, is the empirical evidence on preferences?

The Female Preference

KINDS OF FEMALE PREFERENCES Male traits are sexually selected whenever females bias matings towards some phenotypes, regardless of the basis for the bias. Accordingly, I will use the term "preference" in the broadest possible way. A preference can be caused by cognitive processes that involve the central nervous system, as when the term is applied to humans. More often, though, preferences are caused by other kinds of mechanisms. For example, females of some species mate more often with males that emit higher amplitude signals (e.g. louder or more frequent calls) than others, simply because those signals propagate over a greater area. Parker (101) terms this situation "passive attraction." In the Pacific tree frog, females are attracted to the male that initiates a group chorus. This may be because the chorus leader is easier for the female to locate (136). Physical and neurological properties of females' sensory systems can act as important peripheral filters that bias the types of stimuli that reach the central nervous system (137, 138). Biases in the peripheral and central nervous system are built into every sensory system that females use to find males—eyes are more sensitive to some colors than others, ears are more likely to hear louder mating calls than soft ones. Some preferences do not even involve the nervous system. The mechanics of copulation favor certain male morphologies over others, resulting in sexual selection (e.g. 37, 110). In hummingbird flower mites, females show preferences for certain host plants, which determine with what types of males (in particular, the male host plant preferences) they will mate (25).

Thus, factors as seemingly irrelevant as habitat choice or visual acuity can affect the kind of male a female mates with and so function as preferences that generate sexual selection.

Little is known about the details of how preferences influence the probabilities that different male phenotypes will be mated. Psychophysical studies suggest that some preferences may work by differentially amplifying the perceived strengths of male signals (76, 123). This can result in open-ended preferences, in which the strength of the female's response increases continuously with increases in the male trait (9, 97). The strength of some preferences is believed to depend on the array of males present, in which case expression of the preference is said to be frequency dependent (102). (This should not be confused with frequency-dependent selection on the male trait, which is a universal feature of sexual selection.) An example of a frequency-dependent preference comes from mottled sculpins, in which it appears that females sequentially examine several males and then make a choice based on their relative sizes (35). This kind of preference, which may be quite common in vertebrates, is affected by which males are encountered and by the memory of the female (64). A form of frequency dependent preference that gives rare phenotypes an advantage (the "rare male effect") has been suggested for *Drosophila* and other groups (e.g. 42, 50, 94, 121).

Last, a female's preference may depend not only on her own phenotype and those of the males around her, but on those of other females as well. It has been suggested that the unanimity of preference expressed by females of some species can best be explained by some females copying the mate choice of others (16, 83).

HERITABLE VARIATION IN FEMALE PREFERENCES The simple observation that animals tend to mate with their own species shows that preferences have evolved and so have (or recently had) heritable variation. Many studies have shown female discrimination for males from different geographical races (e.g. 22, 31:p. 325, 92), differences between strains in female preference for males carrying mutants, and differences between the preferences of mutant females (58 and references therein). The locations of some of the genes controlling preference in *Colias* butterflies have been partially mapped (51). Of the direct demonstrations of genetic variation for preference within a population, the most spectacular are the selection experiments on ladybirds by O'Donald, Majerus, and their coworkers (98, 99). They have successfully selected for high and low lines of female preference for a naturally occurring melanic morph of the beetle. In another important selection study, Crossley (26) altered female preferences for the ebony and vestigial mutants in *Drosophila melanogaster*.

There is also negative evidence for genetic variation within species for preferences. Many selection experiments have attempted to produce reproductive isolation between two portions of a laboratory population. Some succeeded (e.g. 106, 108, 127), while others failed (e.g. 114, 122; see also 126). This checkered history suggests that genetic variation for a preference may not always be present. Phylogenetic constraints on the evolution of preferences are imposed by the types of sensory modalities that are already developed in the species (112). For example, wing color is sexually selected in the highly visual butterflies, while pheromones are sexually selected in the olfactorily oriented moths (105). Female mating biases that arise from passive attraction (101) act as preferences that cannot evolve because they arise from the physics of communication (for example, when females are attracted to louder calls simply because they propagate over a larger area).

The data thus show that heritable variation in mating preferences, a prerequisite for all the major theories of sexual selection, definitely exists in some species at some times. Evolution of preferences for certain traits may, however, be constrained by lack of genetic variation at other times.

SELECTION ON PREFERENCES Most of the evidence for selection on preferences is from comparative studies. Many evolutionists believe that the primary force acting on mating preferences is selection to avoid hybridization with other species (e.g. 31), but the suggestion is controversial (91). This type of selection (reproductive character displacement) favors preferences for conspecific males that are as different as possible from other species; these preferences in turn are expected to cause the male traits of sympatric species to diverge from each other. A number of workers have looked for the shift in the male trait by comparing sympatric and allopatric populations (e.g. 10, 36, 46, 81, 107, 132, 134). Trends consistent with character displacement have been found, but the evidence remains equivocal in most cases. A convincing case has, however, been made for floral characters in plants (80). Selection can favor the presence or absence of a preference in a similar way. Kaneshiro (65) has suggested that when males are rare, many forms of preferences are disadvantageous, since they can cause females to miss mating opportunities and go unfertilized. When males are common, selection to avoid hybridization favors the establishment of preferences that allow females to identify conspecific males correctly.

Genes that affect mate preference, like other kinds of genes (31), are expected to have pleiotropic effects on many other aspects of the female. Selection acting on these other characters will have the side effect of selecting for certain preferences. The auditory system of hylid frogs is a very interesting example (138). Females hear calling males using the basilar papilla of the inner ear, which is thought to act as a resonator whose tuning depends on the size of the female. Smaller females are tuned to higher frequencies, larger females to lower frequencies. This tuning affects mate choice because it determines the frequency range of male calls that the female can hear. Female body size obviously evolves under many ecological pressures having nothing to do with mate choice. This will inadvertently have the effect of changing the average female preference in the population. Pleiotropic selection of preferences may be quite common.

CONCLUSIONS ABOUT THE DATA ON PREFERENCES The data on female mating preferences are considerably less complete than those for male traits. In particular, there are no data that speak directly to the controversy. This frustrating situation is in part due to the behavioral and statistical nature of preferences, which make them intrinsically difficult to measure.

If only the evolutionary forces acting on preferences could be directly observed, the critical questions posed by the controversy could be answered empirically. There are three prerequisites to this objective. First, the preference functions (the statistical rules by which females bias their mating towards different types of males) must be characterized; this has not yet been adequately done for any species. Second, differences between individual females in their preference must be quantified. In conjunction with analogous data on the male trait and other relevant characters (already available for some species), those data would make it possible to measure the forces of selection acting on the preference using existing statistical methods (7, 11, 41, 78). We could then determine, for example, if preferences for more viable males are at a selective advantage or not. Third, data on genetic variation in and correlation between these characters is needed, since some hypotheses rely on indirect genetic effects. These three elements would allow one to construct a comprehensive description of the evolutionary forces acting on female preferences.

Empirical methods are not the only possible approach to this controversy, however. The logical consistency of the arguments can be tested using population genetic models of the evolutionary processes involved. This path of inquiry has produced a number of insights into sexual selection by female choice and now allows a number of generalities to be drawn.

THE THEORY

Formal theoretical work on sexual selection was begun by O'Donald, who has studied a large number of models from the 1960s to the present (summarized in 97). He has been joined more recently by a number of other workers, with the result that this is now an active area of research. Detailed reviews of some of these models have appeared recently (5, 6, 71).

Origin of the Preference

The origin of male secondary sexual traits can usually be traced to preexisting structures, such as feathers. The origin of preferences, in contrast, is far more obscure.

The most common origin for preferences may be in preexisting biases inherent in the females' sensory systems. Burley's experiments on female response to novel male phenotypes in zebra finches (17) provide an example of what preexisting preferences may look like. The initiation of sexual selection in these cases may be caused not by the sudden appearance of a preference in a species where there was none before, but by changes in the mating system, ecological conditions, or male traits that allow the preference to be expressed.

Two other important mechanisms for establishing preferences are selection for species recognition and pleiotropy. For example, natural selection will favor new mutants that cause females to mate less frequently with other species, which can secondarily cause preferences for certain types of conspecific males and so initiate sexual selection (45, 52). Selection for species recognition and pleiotropy are also important in the evolution of established preferences and are discussed in that context below.

Another path by which preferences can originate was proposed by Fisher (45). Fisher considered a population in which initially there is no female mate choice. Occasionally, advantageous mutations appear that sweep through the population under the influence of natural selection. If now a preference gene appears that causes females to favor matings with males carrying the advantageous trait, that preference will tend to spread. In modern terms, a genetic correlation (by linkage disequilibrium) develops between the trait and the preference because females with the preference tend to mate males with the trait and so bear offspring that carry both the trait and preference genes. As the trait gene increases in frequency by natural selection, the preference hitchhikes along, increasing as a side-effect (correlated response) of the selection on the trait because of the genetic correlation. Fisher stated that after this initial adaptive period, sexual selection could later cause male traits to become exaggerated to the point where they are maladaptive, i.e. lower male survival. There is no question that Fisher was essentially correct in his argument, which has been verified by formal genetic models (59, 60, 66, 97).

Fisher's idea for the origin of preferences is the prototype of all good genes hypotheses for sexual selection, because it shows how preferences for adaptive male traits can spread. But what is true for a polygynous population that initially lacks any kind of preference turns out not to be true for populations in which alternate forms of preferences exist. Once a preference is established, alternative preference genes favoring deleterious male trait genes can actually spread by the same mechanism if the sexual selection on the male trait they generate is sufficiently strong (59, 60, 66, 97). This is one of the surprising conclusions to come from the growing body of theory on the evolution of established traits and preferences.

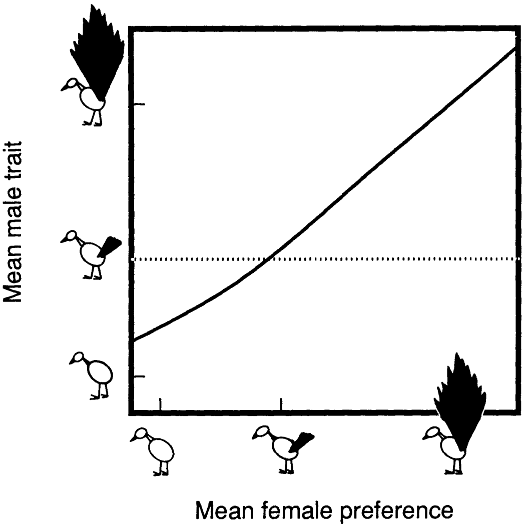
Evolution of Established Traits and Preferences

NULL MODELS A logical first step to understanding the evolution of the trait and preference is to ask how the system works under the simplest conditions. Using this as a null model, we can then proceed to more complex and realistic scenarios. Null models based on continuous and discrete variation, and on a variety of behavioral assumptions, have now been analyzed (66, 76, 79, 117). While the models differ in many details, their qualitative outcomes are strikingly similar. They confirm Fisher's statement (45) that evolution of the preference can result in maladaptive evolution of the male trait, and they reveal some additional features that he apparently did not appreciate.

These models consider a population in which females choose mates freely from among the males and there is unlimited polygyny. In addition, the mating preference is assumed to be free of direct selection, meaning that it does not influence female survival or fecundity. This implies that females do not receive any material benefits, such as parental care or a nest site, from their mates. (This conforms to the natural history of lekking species, in which sexual selection has produced its most flamboyant effects.) The male trait affects survival as well as the chances of mating. Here I will assume there is an intermediate expression of the male trait that maximizes survival. This situation is probably typical, as when changing the length of a bird's tail from its aerodynamic optimum decreases its efficiency.

The null models ask how the preference and trait coevolve under these circumstances. More specifically: Do preferences for the adapted, intermediate males spread through the population, as predicted by the good genes school?

The equilibrium curve The most surprising and interesting result is that there is a continuous range of possible evolutionary outcomes, rather than just a single equilibrium. This is best visualized in a graph that plots the population's average for the male trait against the average female mating preference, as in Figure 1. The equilibria fall along a line or curve on this graph. This finding can be understood as follows. Consider in turn the evolutionary forces acting on the trait and the preference in a population that is at equilibrium at any point on the right hand part of the solid curve in Figure 1. The male trait experiences the antagonistic pulls of natural and sexual selection. Males with the bigger than average tails survive less well but sire more



Schematic of the equilibrium curve for the mean of the male trait and the female preference in the null models (solid curve). The degree of development of the male trait that maximizes survival is indicated by the dashed line.

offspring than males with smaller than average tails; conversely, males with smaller tails survive better but mate less successfully. At an equilibrium, the forces of natural and sexual selection exactly offset each other, so there is no net evolutionary advantage to either kind of male. When the male trait is at equilibrium, there is no net evolutionary force acting on the preference. This follows from the assumption that preferences do not affect the immediate fitness of females.

The good genes school predicts that evolution should favor preferences for adapted (viable) males. The null models show that this is one possible outcome, represented by the intersection of the solid and dashed lines in Figure 1. This possibility, however, is represented by only a single point on the equilibrium curve. In the null models, no point of the equilibrium curve is a priori more probable than any other, and so this adaptive outcome is expected to be exceedingly unlikely. The good genes expectation therefore is not supported by these models.

An equilibrium curve exists even if the trait that females prefer is expressed in both sexes, rather than just in males (66). Again, the force of natural selection (now acting in both sexes) is offset by a force of sexual selection (acting only on the males) at an equilibrium. Given the appropriate genetic variation, however, the trait will tend to become sexually dimorphic, lying at its natural selection optimum in females but displaced from the optimum in males by sexual selection (75, 79). The existence of the equilibrium curve is insensitive to the type of preference females express and appears regardless of whether the preference is open-ended, relative, or absolute, frequency-dependent or independent, etc.

Some discussions, based on the assumption that sexual selection inevitably reinforces natural selection, have concluded that genetic variation for the male trait would rapidly become exhausted (12, 34, 89, 140). The null models show that at equilibrium, the balance of natural and sexual selection results in an overall pattern of stabilizing (rather than directional) selection on the male trait, as occurs in many nonsexually selected traits. There is therefore no general theoretical basis for thinking male traits should have lower amounts of genetic variation than other kinds of characters. This accords with the data, which show typical heritabilities for the large majority of male secondary sexual traits that have been studied, including behavioral traits (e.g. in fish: 44, 92; in insects: 18, 21, 23, 84). While the discussion thus far has assumed that both the preference and the trait are inherited genetically, these characters can also be inherited culturally (through learning) (e.g. 30). Models based on cultural inheritance can have an equilibrium curve and other behaviors analogous to the models that assume genetic inheritance (15).

In the absence of additional evolutionary forces, a population will remain at equilibrium at any point on the curve without evolving either up or down the curve. Fisher's good gene scenario for the origin of preferences does not apply once preferences for deleterious male traits appear by mutation, because those preferences can offset the natural selection favoring adaptive male trait genes. On the other hand, the preference and trait will not become more exaggerated, so the evolutionary forces described thus far cannot explain increased elaboration of trait and preference. Other forces must be responsible, a point to be discussed below.

How do populations evolve when they are not on the equilibrium curve? There are two possibilities. Either the population will evolve to a point somewhere on the equilibrium curve, in which case the curve is said to be stable, or it will evolve away from the curve, in which case it is unstable. The outcome depends on a number of behavioral and genetic variables. Under a wide range of conditions, the equilibrium curve is stable. In this case, the point on the curve to which the population will evolve depends not only on genetic, behavioral, and ecological parameters, but also on the initial state of the population. This suggests the very interesting possibility that very similar species may evolve to different states (that is, different points on the curve) because of purely historical factors.

One can ask how the population will evolve if, for some reason, the trait or preference is constrained from evolving by lack of heritable variation. If the trait is constrained, there will be no evolutionary force acting on the preference, and it will not change. If the preference is constrained, the population will evolve to that point on the equilibrium curve that corresponds to the existing strength of the preference. For these reasons it is convenient to think of the trait as the dependent variable and the preference as the independent variable, as they have been graphed in Figure 1. (In some papers, though, the axes are reversed, and readers should be aware of this cosmetic discrepancy.) The data on the heritability of preferences (discussed above) suggest that constraints on the preference are likely to be much more common than constraints on the trait in natural populations.

Fisher's runaway process Under certain conditions, theory predicts that the equilibrium curve will be unstable, in which case the population will rapidly evolve away from it. One way in which the curve can be rendered unstable involves Fisher's famous "runaway process" (45, 76). A runaway is triggered when the preference is displaced from its equilibrium. This causes the male trait to change, since the forces of natural and sexual selection are no longer in balance. Evolution of the male trait causes a further change in the preference because of the genetic correlation between the two. If the genetic correlation is sufficiently large, the process will snowball: The altered preference selects for even greater elaboration of the male trait, and so forth. This positive feedback continues until the patterns of selection or genetic variation change sufficiently, or the population goes extinct (45, 76). In any event, the male trait will evolve rapidly, maladaptively, and in an unpredictable direction.

A runaway process will be initiated if the genetic correlation between the preference and trait becomes sufficiently large. The correlation thus affects the stability of the equilibrium curve but does not affect its existence or location. In general, a genetic correlation can result from linkage disequilibrium or pleiotropy. Positive linkage disequilibrium is the statistical association of genes for the preference and trait. It is expected to arise spontaneously with sexual selection because females with preferences for long tails (for example) tend to mate males with long tales; conversely, females that prefer short tails mate with males bearing short tails. The offspring then tend to inherit those combinations, and this results in the genetic correlation (66, 76, 97). Pleiotropy, in which genes simultaneously influence expression of both the preference and trait, could cause either a positive or negative genetic correlation between the trait and preference. Mechanisms for pleiotropic coupling between the preference and trait have been suggested by several empirical workers (e.g. 2, 33, 62, 74), but definitive data are lacking.

There is a second path, distinct from the runaway, by which the curve of equilibrium can become unstable. Certain forms of frequency-dependent preferences render the equilibrium for the male character unstable, even if there is no genetic correlation and the preferences do not evolve (24, 97, 117). This again leads to rapid maladaptive evolution of the male trait.

Conclusions from the null models The message from the null models is that sexual selection alone does not cause the female mating preferences for more viable males to sweep through the population. Even when females can accurately discriminate between high viability and low viability males, a preference for a deleterious type of male can persist, producing sexual selection that maintains the less viable males in the population. This is maladaptive in that it reduces the mean survival of males in the population.

How can this be reconciled with the common notion that selection results in adaptation? The most transparent rationale first considers the male trait, which experiences two forms of selection. Natural selection favors one form of the trait, while sexual selection favors another, with the result that the trait equilibrates at a compromise between the two. Once this occurs, there is no net evolutionary force acting on the preference, since females preferring males with longer tails have sons that survive worse but mate more successfully, while females preferring males with shorter tails have sons that survive better but mate less successfully. Evolution therefore does not favor preferences for more viable kinds of males. There are two additional rationalizations for the maladaptive outcome. The first of these compares the number of evolutionary "degrees of freedom" with the number of characters under selection (69). Given two degrees of freedom (the trait and the preference) but only one selective constraint (selection acts directly only on the trait), there is a residual degree of freedom. This results in a continuum of equilibria rather than a single point. The final rational is based on the fact that sexual selection necessarily involves frequency-dependent selection. It is well known that this type of selection can lead to a decline in the fitness of a population (142).

The most prominent feature of the null models is the equilibrium curve. The existence of multiple equilibria suggests that the evolutionary history of a population is very important in determining its evolutionary fate, since the initial state of the trait and preference determines the point on the equilibrium curve to which the population will evolve. For most real populations, however, the preference may be under some form of direct selection, contrary to the assumption of the null models. This eliminates the neutral stability of the preference (which is the cause of the equilibrium curve) because now one form of the preference is evolutionarily favored. The equilibrium curve nevertheless has two useful roles. First, it shows that evolution does not invariably favor females that prefer to mate with males carrying "the ideal genetic material" (129), if "ideal" means best adapted to the environment. This finding is fatal to the simplest of the good genes hypotheses. Second, the curve is a heuristic aid for understanding the evolutionary outcomes in situations where the preference is under selection, as will now be discussed.

DIRECT SELECTION ON PREFERENCE GENES While the theoretical possibility that an unstable equilibrium curve can cause a runaway process is very interesting, it is important to realize that many other mechanisms can lead to extreme development of the preference and trait. Even when the curve is stable, several evolutionary forces can cause the preference to become more extreme. The result is that the population will evolve along the curve in a process that might be termed a "walkaway" (in contrast to Fisher's "runaway").

One important such mechanism is direct selection on preferences, which occurs whenever they affect the survival or fecundity of females. Although direct selection on preferences has yet to be directly observed, theoretical expectations for its effects have been obtained from extensions of the null models.

Reproductive character displacement, whose uncertain empirical status was mentioned earlier, is a form of direct selection that has not been well studied by theoreticians. Intuition suggests that this type of selection on the preference would favor that form of the preference that minimizes hybridization. The equilibrium for the male trait would then lie at the corresponding point on the equilibrium curve derived from the null models described above.

Selection on traits unrelated to mating can alter (or even initiate) preferences through pleiotropy. The eyespot responses, well-known in many animals, may have originated through natural selection for detection of predators and prey. Ridley (109) speculates that the eyespot response of female peacocks has inadvertently led to sexual selection for the eyespots on the tails of males. The example of auditory tuning in hylid frogs was discussed earlier. Selection on pleiotropic effects is adaptive for the females, in that natural selection will generally enhance their fitness, for example, by increasing predator detection. The consequences for the male trait, however, are not expected to be adaptive, since the trait will often be made conspicuous to predators as well as to females.

Direct selection on preferences also occurs when a female's immediate fecundity is affected by the kind of male she mates. Males of many species provide females with parental care or with resources such as food and oviposition sites that have a large effect on female reproductive success (reviewed in 29, 53, 115, 128). Females will also be selected to avoid males that have low fertility (reviewed in 53, 128) or that carry contagious diseases (47). In these situations, genetic models show there will be a single evolutionary equilibrium, which corresponds to the point that maximizes immediate female fecundity (68). Depending on the ecological conditions, this can be either at the point that maximizes male survival or at some other point. This assumes females are choosing on the basis of male phenotypes, rather than the resources provided by the males. In many species females are likely to be selecting resources directly, rather than indirectly through a phenotype of the male (e.g. 1, 104), leaving males to compete among themselves for control of the resources (53, 115).

Costs associated with finding males are another source of direct selection on preferences in some species (101). Consider species in which females spend substantial time and energy searching for males. Females that prefer conspicuous male phenotypes may expend less energy and have a lower risk of predation than those searching for more cryptic kinds of males. While most discussions of sexual selection assume the preference determines the evolutionary fate of the trait, search costs can reverse the direction of causality: The preference will be selected to track evolutionary changes in the male trait that are caused by other ecological factors. Models that incorporate search costs show that their effect is to favor preferences that minimize the time, energy, and risk that females expend (71). If all forms of the male's advertisement signal propagate equally well through the environment, the evolutionary equilibrium lies at the point that maximizes male survival. More generally, though, the equilibrium lies elsewhere. In particular, if some kinds of signals (e.g. certain call frequencies) propagate better through the environment, females will evolve preferences for them and so minimize their search costs, even when such signals increase male mortality by attracting predators.

The evolutionary equilibria discussed above are not the only possible evolutionary outcomes in models with direct selection. As in the null models, there is the possibility of an unstable runaway process. This would cause a population to evolve rapidly away from the equilibrium, resulting in a decline in the population to evolve rapidly away from the equilibrium, resulting in a decline in the population's mean fitness and perhaps even its ultimate extinction (68, 71).

Having now reviewed the theory pertaining to various forms of direct selection, a simple unifying rule for the evolutionary equilibria becomes apparent. The equilibrium curve found in the null models is replaced by a single point of equilibrium. That point is where total female fitness (the product of survival and fecundity) is maximized. The equilibrium for the male trait is at the point on the null model's equilibrium curve (Figure 1) that corresponds to this degree of development of the preference. As before, the trait lies at a compromise between what is favored by natural selection and what is favored by sexual selection. Under special circumstances, natural and sexual selection will favor the same thing, and the outcome of evolution is adaptive. More often, however, natural and sexual selection are expected to favor different forms of the trait, and the trait will be displaced from the condition that maximizes male survival.

OTHER EVOLUTIONARY FORCES ACTING ON PREFERENCES Individual selection is not the only force causing characters to evolve, and mating preferences are no exception. Two other forces have been studied in the context of sexual selection: genetic drift and group selection.

Random genetic drift is constantly at work in all natural populations. While its effects may be small for many types of characters, theory suggests it could be unusually important in the context of sexual selection. The genetic correlation between the trait and preference greatly magnifies the effect of drift acting on the preference (77, 95, 143), causing the population to evolve in an unpredictable direction along the equilibrium curve at an accelerated rate (76).

Seger & Trivers (118) have shown how group selection can drive mating preferences in an adaptive direction. Sexual selection can generate the variation in the fitness of local demes on which group selection acts if the sexually selected trait influences the deme's reproductive output. Even if evolution within demes does not favor adaptive combinations of the trait and preference, proliferation of better adapted demes can cause a preference for more viable (i.e. adapted) males to spread through the species. This is therefore a directional force that favors adaptive evolution of the preference and trait. Group selection remains a controversial topic in evolution (141), and the strength of its effects on sexual selection is an open empirical question.

GOOD GENES MODELS Results from the theory described so far do not support the good genes expectation that preferences for more viable male types usually will spread. Those models, however, do not explicitly incorporate the additional assumptions on which the second-generation good genes arguments are based. Recent models have begun to address this deficiency.

Recall that Zahavi's handicap mechanism (144) involves not only a preference and a male trait that reduces survival (the handicap), but also a third character that influences general viability. Mature males whose handicap trait is extreme also will tend to carry good genes for the general viability character, since otherwise they would have died under the dual burdens. This is then supposed to favor preferences for handicapped but otherwise high viability males, because females with these preferences bear high-viability offspring. Several workers have independently constructed different genetic models of the handicap mechanism. These have all been shown to produce the same qualitative outcome (69). The viability character ultimately uncouples itself from the trait (despite their correlation) and evolves to whatever equilibrium natural selection favors. The equilibria for the handicap trait and preference fall along a curve like that found in the null models, again usually resulting in a maladaptive outcome. These findings provide no support for the handicap hypothesis: The trait and preference are free to evolve to a maladaptive equilibrium, and no evolutionary force favoring an adaptive preference is generated.

Hamilton & Zuk (55) have suggested a more complex hypothesis based on the idea that the coevolution of a species with its pathogens and parasites prevents an evolutionary equilibrium from ever being reached. Disease can affect the expression of the male trait (for example, sick males have duller plumage). While the pathogen responsible for variation in the male trait changes as different diseases sweep through the population, at any moment the brightest males will be those that are most resistant to the current pathogen. Female preferences for bright males will become genetically correlated with whatever resistance genes are currently favored, and they will increase in the population as the resistance genes do. The hypothesis envisions adaptive evolution because the preference promotes increase of whatever resistance genes are currently advantageous, while the male trait becomes exaggerated as a side effect. Hamilton's proposal has been investigated with a simplified genetic model (70). The changing regime of natural selection resulting from the introduction of new pathogens causes the equilibrium curve of the null models to be lost. It is usually replaced by two distinct evolutionary outcomes. Under certain initial conditions, the preference and trait increase, as predicted by the hypothesis. On the other hand, some initial conditions, including those when the trait and preference are rare, do not lead to the predicted outcome. Furthermore, the mean population fitness does not increase with time as predicted. The model thus does not confirm several important aspects of the parasite hypothesis, but further study is needed.

Two interesting proposals for good genes mechanisms have been dubbed the age-indicator and total-viability concepts (14). The age-indicator hypothesis suggests that female preferences for older males will be favored (e.g. 52, 86, 129), while the total-viability hypothesis states that preferences for males carrying the fewest deleterious genes in their genomes will be favored (e.g. 12, 85). In the age-indicator hypothesis, females that mate young males can expect to mate with individuals carrying the average number of mutations, since natural selection has not yet had time to act on the viability differences between males. Females that mate older males, however, will tend to mate with individuals carrying few mutations, since only those males survive long. The preference for older males then becomes correlated with high-viability genes that are spreading through the population, and thus it hitchhikes to higher frequencies as in Fisher's scenario for the origin of the preference. As with the Hamilton-Zuk proposal, this mechanism for the preference prevents alternative preferences from maintaining deleterious male traits (as they do in the null models) because females cannot detect the individual alleles that a male carries, only his age. The total viability hypothesis works in a very similar way but assumes females choose on some basis, other than age, that indexes the number of deleterious mutations males carry.

These ideas warrant analysis by formal genetic models to determine if the mechanisms work as proposed. Two specific questions need to be answered. First, do these mechanisms indeed promote the evolution of preferences for adaptive males? It may be, for example, that the forces generated by these mechanisms actually produce preferences for maladaptive male traits. Second, will the trait that females use to choose between males tend to become uncoupled from age or viability (as the handicap and viability characters do in the handicap mechanism)? If this is possible, the trait and preference may again coevolve with the preference in the maladaptive way described by the null models.

Generalizations from the Theory

Genetic models of sexual selection show that even when females have the ability to discriminate between forms of the male trait that influence survival, evolution does not inevitably favor preferences for adaptive males. In fact, a variety of mechanisms can establish preferences for deleterious male traits, causing sexual selection to maintain males in an ecologically maladapted state. Inclusion of additional characters that affect viability, as suggested by the handicap and other hypotheses, does not alter this qualitative picture. At an evolutionary equilibrium, immediate female fitness is maximized. There is no support for the notion that future "genetic benefits" affect the evolutionary equilibrium for the preference.

Theory shows there are several mechanisms that will tend to cause the evolution of conspicuous and deleterious male traits. Passive female attraction favors male signals that attract females over the largest areas. The evolutionary effect of search costs favors the preference that minimizes the time, risk, and energy females expend finding mates—again, a type of preference that selects for male traits that are conspicuous. Selection for females to avoid hybridization favors preferences for traits that are distinct from those of other sympatric species, which may lead to the exaggeration of the male trait. Finally, even in the null models, evolution of the male trait along the equilibrium curve will often produce traits that are conspicuous: Crypsis relies on a delicate balance of behavior, morphology, and coloration, and any deviation from the optimal combination produces a more conspicuous phenotype. These four mechanisms may account for many of the cases in which sexual selection has resulted in conspicuous male traits.

Taken together, results from the theory show that diverse outcomes for the joint evolution of the trait and preference are possible. Even in cases where direct selection acts on the preference and reduces the evolutionary equilibrium to a single point, the male trait may ultimately lie near to or far from its ecological optimum, depending on the details of how the ecological conditions act on the preference. It is therefore very difficult to make broad generalizations that can be tested using only information about the male trait.

CONCLUSIONS

While the dispute between the nonadaptive and good genes views of sexual selection has not been resolved, it provides a continuing stimulus for research in the area. The ultimate goal is an understanding of sexual selection based on processes that have been demonstrated by observation and experiment, and on logic that has been verified by genetic models.

The nonadaptive school now has a theoretical foundation showing that preferences and traits can often be expected to coevolve in maladaptive ways. This expectation is supported by the many studies that have found exaggerated male traits to be detrimental to survival. Studies showing that females favor more viable males (which some argue are counterexamples to predictions of the nonadaptive school) have not controlled for the variation in other characters correlated to the male trait, such as health and vigor. Several specific good genes hypotheses claim that such correlations will cause preferences to evolve in an adaptive way, but these are not supported by analyses of detailed genetic models. However, some propositions remain to be evaluated.

The good genes school at present lacks a validated theoretical basis and has yet to identify empirical observations that might compel one to reject the view of the nonadaptive school. The good genes view is grounded in the general intuition that evolution is adaptive, and the specific idea that the larger, more conspicuous, and more vigorous males often favored by sexual selection must be better in some sense. This motivates the continued search for hypotheses that are consistent with that view, as well as with logic and the data. The enterprise has not yet been successful, although the possibilities have not been exhausted.

This controversy has parallels with other developments in modern evolutionary biology. The reconsideration of early evolutionary arguments based on naive versions of group selection shows that individual selection often favors characters that increase each individual's ability to compete against others, at the expense of adaptation to the ecological environment (139). The introduction of game theory into studies of animal behavior led to an increased appreciation of how selection can favor many forms of interference and competitive behavior (90). Both of these developments revealed specific processes that cause the degree of adaptation, in terms of the average fitness of individuals in the population, to decrease. This review suggests that sexual selection may be yet another way by which adaptation is compromised by selection.

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